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ORIGINAL ARTICLE

Variation between plant species in pollen digestion rates in the green lacewing *Chrysoperla carnea*

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Abstract

Pollen are an important food source for numerous insects and may be used as natural markers in ecological studies. However, to make inferences about the movement rates of insects based on their gut contents, information on pollen digestion rates is needed. Here, we assessed how the consumption and digestion rates of pollen ingested by *Chrysoperla carnea* Stephens (Neuroptera: Chrysopidae) adults are influenced by plant species, temperature, and sex. We offered pollen of two insect-pollinated plants – *Acer pseudoplatanus* L. (Sapindaceae) and *Helianthus annuus* L. (Asteraceae) – and two wind-pollinated plants – *Fraxinus excelsior* L. (Oleaceae) and *Quercus rubra* L. (Fagaceae) – differing in size and protein content, to adult lacewings at two temperatures, 20 and 25 °C. After feeding, lacewings were allowed to digest pollen for up to 14 days, sampled at 10 time intervals. At each of these intervals, lacewings were frozen and the internal pollen were obtained through acetolysis and quantified under a light microscope. The number of pollen grains decreased exponentially over time and declined faster for *Acer* than for the other three plant species. The half-life and the time at which 95% of the pollen grains were digested were lower for *Acer* than for the other plant species. Lacewings consumed more pollen grains from *Acer* and *Quercus* than from *Fraxinus* and *Helianthus*. Male lacewings consumed 30% fewer pollen grains than females, but without differences in their digestion rates. Our results show that lacewings consumed higher amounts of high-protein pollen (*Acer* and *Quercus*) and that digestion rates differed among plant species, which could be linked to their structural characteristics. The variable digestion rates of pollen grains may influence the study of lacewing diet composition. Studies that make inferences about the pollen diet or movement ecology of lacewings by analysing their gut contents should account for species-specific pollen digestion rates.

KEYWORDS
Acer pseudoplatanus, *Chrysoperla carnea*, Chrysopidae, common green lacewing, digestion rate, feeding ecology, *Fraxinus excelsior*, *Helianthus annuus*, natural marker, Neuroptera, pollen feeding, *Quercus rubra*

INTRODUCTION

Pollen are an important and ubiquitous food source for a wide range of insect species, including pollinators, predators, and parasitoids (Roulston & Cane, 2000). As pollen grains are highly resistant to breakdown and have distinctive morphological characteristics that allow their identification to family, genus, or species level, they can

be used as natural markers in ecological studies (Jones & Jones, 2001; Silberbauer et al., 2010). The pollen consumed by or attached to insects were successfully used to study the diet, habitat use, and movement patterns of insects (Silberbauer et al., 2010). For example, pollen of specific plants were used to assess dispersal distances in moths (Del Socorro & Gregg, 2001) and hover flies (Wratten et al., 2003). Information on digestion rates of pollen in insect guts can improve our understanding of the pollen diet and movement rates of the studied insect.

The common green lacewing, *Chrysoperla carnea* Stephens (Neuroptera: Chrysopidae), is a ubiquitous insect in agricultural landscapes of Europe and Asia (Duelli, 2001). Whereas lacewing larvae are important predators of pests in several crops (McEwen et al., 2007), adults feed mainly on pollen and nectar (Canard, 2001). Adult lacewings are generalists that consume pollen from a wide range of wild trees and herbs (Bertrand et al., 2019), sown flower strips (Alcalá Herrera et al., 2022), and crops (e.g., olives, oilseed rape, carrot, and alfalfa; Villenave et al., 2006; Villa et al., 2019). Whereas the range of pollen used by lacewings is already well-known, information on the time span that consumed pollen grains remain detectable in lacewing guts is largely lacking. Li et al. (2010) found that, after feeding on maize pollen for 2 days, the number of pollen grains in lacewings' guts decreased by about 35% after 9 h, but on average more than 3000 grains were still detected per individual. We are not aware of any detailed evaluation of pollen detectability in lacewings across longer periods of time.

Pollen consumption and digestion may be affected by various factors. First, females may ingest more pollen than males (Villenave et al., 2005; Alcalá Herrera et al., 2022), as they have higher nutritional and energetic needs, though digestion rates may not differ between females and males because there is no sexual size dimorphism in this species. Second, as temperature influences insect metabolism (Abram et al., 2017), higher temperatures may give rise to faster digestion due to higher proteolytic activity, as has been observed in bees (Crailsheim et al., 1993). Finally, the properties of pollen may influence digestion rate. For instance, nutritional value and protein content of pollen grains vary among plant species and the digestion rate of pollen with high nutritional value may be faster than that of pollen with lower nutritional value (Roulston & Cane, 2000; Roulston et al., 2000). In addition, pollen structure may influence their digestion rate. For example, structurally simple, thin-walled maize pollen grains are more rapidly digested than structurally complex sunflower pollen in a flower beetle (Human & Nicolson, 2003). The size of pollen grains may not necessarily influence the digestion rate because wall width is not related to grain size, but pollen grain size could influence the amount of pollen consumed to reach the satiation level. Furthermore, pollen from insect-pollinated plants may also be preferred above pollen dispersed by wind due to co-adaptation and presence of nectar rewards, although the protein concentration of pollen grains from insect- and wind-pollinated plants overlaps strongly (Roulston et al., 2000).

Here, we assessed how the consumption and digestion rates of pollen ingested by *C. carnea* adults are influenced by plant species, temperature, and sex. We used pollen of two insect-pollinated plants – *Acer pseudoplatanus* L. (Sapindaceae) and *Helianthus annuus* L. (Asteraceae) – and two wind-pollinated plants – *Fraxinus excelsior* L. (Oleaceae) and *Quercus rubra* L. (Fagaceae) – that differ in size and protein content and that are frequently consumed by *C. carnea* in Western Europe, and included two temperature treatments (20 and 25 °C). We expected that consumption and digestion rates would be higher at 25 than at 20 °C, and higher for pollen from insect-pollinated than from wind-pollinated plants. Furthermore, we predicted that females would consume more pollen than males due to their higher protein needs for egg production, but that digestion rates of males and females would not differ. Information on the time span that pollen grains are detectable in lacewing guts can extend data from pollen marker studies by allowing the conversion of estimates of movement distances to movement rates.

MATERIAL AND METHODS

Lacewing rearing

Adult *C. carnea* were reared from commercial lacewing larvae (ÖRE Bio-Protect, Schwentinental, Germany) in climatic chambers at 25 °C, 65% r.h., and L16:D8 photoperiod. First and second instars were placed in separate glass Petri dishes (9 cm diameter) to prevent cannibalism. A cotton ball soaked in water was added to each Petri dish to prevent desiccation. Larvae were fed with *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) eggs (Royal Brinkman, Straelen, Germany) that were replaced every 3–4 days until lacewings reached the pupal stage. At that moment, food was removed from the Petri dish and only the wet cotton was maintained. Freshly emerged adults were starved for 24 h before starting the feeding trials.

Pollen feeding trials

Adult lacewings were offered pollen of one of four plant species that are known food sources of field populations of *C. carnea* (Bertrand et al., 2019). Insect-pollinated plants were represented by sunflower (*H. annuus*) and sycamore (*A. pseudoplatanus*) and wind-pollinated plants by northern red oak (*Q. rubra*) and common ash (*F. excelsior*). The pollen grains of these species differ in size and protein content. Whereas all four pollen types are classified as medium-sized grains, *Helianthus* has the largest grains (44.7 μm mean diameter), followed by *Quercus* (36.7 μm), *Acer* (38.4 μm), and *Fraxinus* (23.7 μm) (Beug, 2004). Pollen protein content is not related to pollination mode and is highest in *Acer* (41.8%), followed by *Quercus* (40.6%), *Fraxinus* (33.3%), and *Helianthus* (30.6%) (Roulston et al., 2000). *Helianthus* pollen

were manually collected from flower strips and sunflower fields in the surroundings of Landau in der Pfalz (Rheinland-Pfalz, Germany) and were dried at room temperature for 7 days. *Acer*, *Quercus*, and *Fraxinus* pollen were purchased from the company Bonapol (České Budějovice, Czechia). All pollen was maintained at −5 °C until use.

An experiment with four factors was conducted: plant species (four levels), temperature (two levels, 20 and 25 °C), sex (two levels), and digestion time (10 levels). For the digestion time, lacewings were allowed to feed and digest pollen for 0 (positive control), 0.33 (8 h), 1, 2, 3, 4, 5, 7, 10, or 14 days. For each combination of time span, temperature, and plant species, at least six individuals were used (three males and three females, if possible; Table S1). We included a negative control in which lacewings were offered only water (three individuals for each combination of plant species and temperature).

Each lacewing was placed on a clean Petri dish containing a wet cotton ball and the top of a 2-ml Eppendorf tube filled with 5 mg of pollen (Figure S1). Lacewings were allowed to feed on the pollen for 24 h. After feeding on pollen, individuals for each time interval treatment were transferred to a clean Petri dish containing a wet cotton ball and an additional cotton ball embedded with a 2 M sucrose solution. Both water and sugar were replaced every 2–3 days. At the appropriate time intervals, lacewings were transferred to labelled Eppendorf tubes and frozen at −5 °C to stop the digestion process.

Pollen extraction and quantification

To extract the pollen grains consumed and retained by lacewings, we used a slightly modified version of the acetolysis process described by Jones (2014), which was successfull to obtain pollen from lacewings in other studies (Villenave et al., 2005; Bertrand et al., 2019; Alcalá Herrera et al., 2022). The wings and legs of the frozen lacewings were removed and the sex of each individual was determined under a binocular microscope based on the number of visible sternites, following San Martin (2004). To remove the pollen grains that might be attached to the outer surface of the lacewings, we placed each individual in separate 2.5-ml plastic tubes with 1.5 ml 70% ethanol and used a Schalltec S20 ultrasonic bath (60 W; Emag, Mörfelden-Walldorf, Germany) at room temperature for 15 min. Afterwards, lacewings were crushed in a clean 15 ml-centrifuge tube with 3 ml of 95% ethanol using a clean glass rod and subsequently vortexed for 3 min at 1060 ***g***. After that, the supernatant was decantated and steps 2–7 of the acetolysis protocol of Jones (2014) were followed using 3 ml of the acetolysis mixture (a 9:1 ratio of acetic anhydride and sulfuric acid). Chemicals were obtained from Carl Roth (Karlsruhe, Germany). Based on preliminary trials, we used a cooking period of 7 min in the heating blocks. After centrifuging the last ethanol rinse, the supernatant was carefully decantated and 50 µl of 50% glycerol was added to each sample.

To count the pollen grains of each lacewing, each sample was vortexed and 25 µl was placed on a microscope slide along with a small amount of Safranin O stain and mixed using a clean plastic rod. Finally, the slides were covered and sealed with melted paraffin wax around the cover slip. One microscope slide was made for each sample and the pollen grains were counted at 400× magnification using an Axiostar light microscope (Zeiss, Zaventem, Belgium). For samples with more than 500 pollen grains, only one quadrant was counted and the number was multiplied by four to obtain an estimate of the total number of grains. Although the number of pollen grains detected in an individual reflects both digestion and defecation, we refer to 'pollen digestion' and 'digestion rate' for simplicity. Negative and positive controls showed that feeding trials worked properly, despite minor contamination in a few individuals of the negative control treatment (mean ± SD = 1.76 ± 2.82 grains for negative controls and 2094.99 ± 2132.67 in positive controls).

Data analysis

To analyse the influence of digestion time (in days), temperature, sex, and plant species on the number of pollen grains in lacewing guts we used generalized linear models (GLMs) with a negative binomial error distribution due to overdispersion of the data. These four experimental factors and all pairwise interactions were included as independent variables. Positive controls were coded as 0 days after feeding. The negative binomial distribution belongs to the exponential family (Zuur et al., 2009) and, due to its log link, allows to model the exponential decay of pollen grains across time in our data set.

Starting from a full model including all experimental factors and their interactions, we simplified the model by removing non-significant interactions using likelihood ratio tests. Analyses were performed in R v.4.0.5 (R Core Team, 2019) using the package 'glmmTMB' (Brooks et al., 2017). Model residuals were evaluated using the package 'DHARMa' (Hartig, 2021). Using the simplified model, for each plant species we determined the half-life of pollen grains and the 95% pollen digestion interval – i.e., the times at which 50 and 5% of the pollen grains were still detectable, respectively, calculated as the time at which the model predicted a number of pollen grains equal to 50 and 5% of the intercept of each plant species using the 'predict.glm' function in R. Finally, we used a binomial GLM to test for the effects of time after feeding on the probability of finding an individual with no pollen grains on its guts for all plant species combined. For this, a logistic regression was used where lacewings without pollen grains were coded as 'success' in the response variable, and lacewings with at least one pollen grain as 'failure'.

RESULTS

The number of pollen grains detected in lacewings decreased exponentially over time (χ^2 = 274.05, d.f. = 1,

P<0.001) and was influenced by plant species (χ^2 = 34.42, d.f. = 3, P<0.001) and sex (χ^2 = 22.72, d.f. = 1, P<0.001) (Table S2). The number of *Acer* pollen grains declined faster than that of the other three pollen types (significant time*plant species interaction: χ^2 = 7.82, d.f. = 3, P = 0.048) (Figure 1), although the difference between *Acer* and *Fraxinus* was only marginally significant (Table S2). Moreover, the intercepts for each plant species indicated that lacewings consumed more pollen grains from *Acer* and *Quercus* than from *Fraxinus* and *Helianthus*. Temperature did not affect the number of pollen grains directly (χ^2 = 22.72, d.f. = 1, P = 0.48) but there was a significant temperature*plant species interaction (χ^2 = 8.24, d.f. = 3, P = 0.041), indicating that the differences in pollen intake depended on temperature. At 25 °C, more *Quercus* and *Helianthus* pollen were consumed than at 20 °C, whereas the consumption of *Acer* was similar at both temperatures and *Fraxinus* consumption declined with higher temperature (Figure S2). Finally, male lacewings consumed 30% fewer pollen grains than females, but digestion rates of male and female lacewings were not distinguishable (Figure S3).

The half-life of *Acer* pollen grains was 3.11 days, whereas *Fraxinus* (4.25), *Helianthus* (4.56), and *Quercus* (4.62) had somewhat longer half-lives. Similarly, the 95% pollen digestion intervals indicated that the last 5% *Acer* pollen were still detectable after 13.43 days, whereas the predicted 95% pollen digestion intervals of *Fraxinus*, *Helianthus*, and *Quercus* exceeded 18 days (18.38, 19.71, and 19.97 days, respectively). Regardless of the plant species, the probability of finding a lacewing without pollen grains increased with time (Figure 2, Table S3) and the percentage of lacewing individuals with no pollen grains ranged from <3% on the first 2 days up to 29.8% after 14 days.

DISCUSSION

The identification of the pollen types ingested by insects can provide valuable insights about the insects' host plant species, habitat use, and movement distances in agricultural landscapes. In addition, information about the pollen digestion rates allows making inferences about movement rates. We evaluated pollen digestion in *C. carnea* during a period of 2 weeks and found that pollen digestion, measured indirectly by quantifying pollen detectability in a time series, showed a pattern similar to an exponential decay, with a relatively fast decline during the 1st days after feeding, and a slow and asymptotic decline afterwards. Plant species significantly influenced the digestion rate, being faster for *Acer* than for *Fraxinus*, *Helianthus*, and *Quercus*. The half-life and 95% pollen digestion intervals of *Acer* grains were around 1 day shorter than for *Fraxinus*, and 5–6 days shorter than for *Helianthus* and *Quercus*. These differences may arise from the structural characteristics of pollen grains. Although the pollen grain size and wall width of the four plant species are similar and the aperture is the same (tricolpate grains), the elongated apertures (colpi) in *Acer* tend to be larger than in the other three (Beug, 2004), which may facilitate the digestion process by enzymes (Roulston & Cane, 2000). Variation in pollen digestion rates across plant species may bias the assessment of pollen diet, because persistent pollen types become overrepresented relative to pollen that are more quickly digested. Therefore, information on plant species-specific pollen digestion rates could improve diet information derived from gut contents.

The half-lives of the four pollen types ranged from 3.11 to 4.62 days, indicating that most of the pollen grains were digested within a period of approximately 5 days after consumption. However, around 70% of the individuals still have pollen in their guts even 2 weeks after their last pollen meal. This has important implications for studies of lacewing dispersal and habitat use because it indicates that a field-collected individual may have consumed a certain resource in the previous weeks and, depending on the time of the year and its reproductive status, it may have moved for long distances within that period (Duelli, 1980, 1984, 2001). Therefore, care should be taken when inferring movement rates from

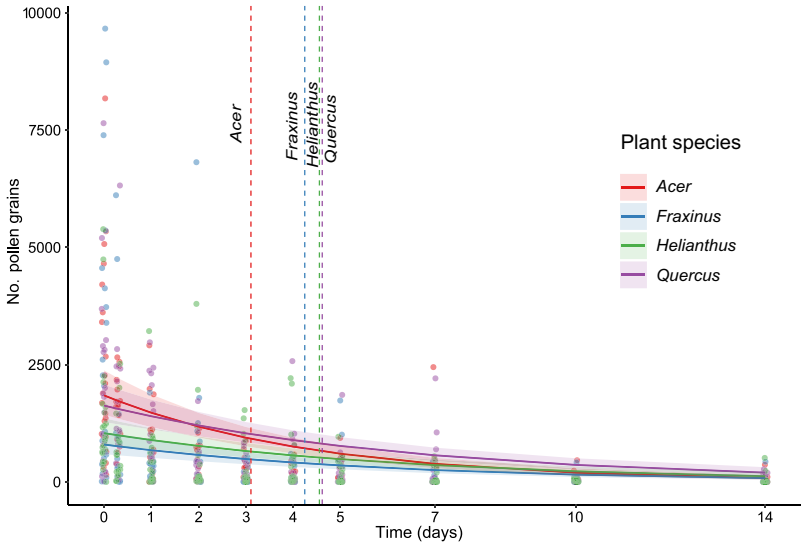

FIGURE 1 Decrease of the number of grains detected in *Chrysoperla carnea* guts over time for pollen of *Acer pseudoplatanus*, *Fraxinus excelsior*, *Helianthus annuus*, and *Quercus rubra*. The coloured dots represent individual plant samples of the various species, the coloured lines represent fitted regression lines based on means, and the coloured shadings indicate 95% confidence intervals. The dashed lines indicate the half-life of each pollen type (that is, the time span at which the pollen load is reduced to 50% since consumption).

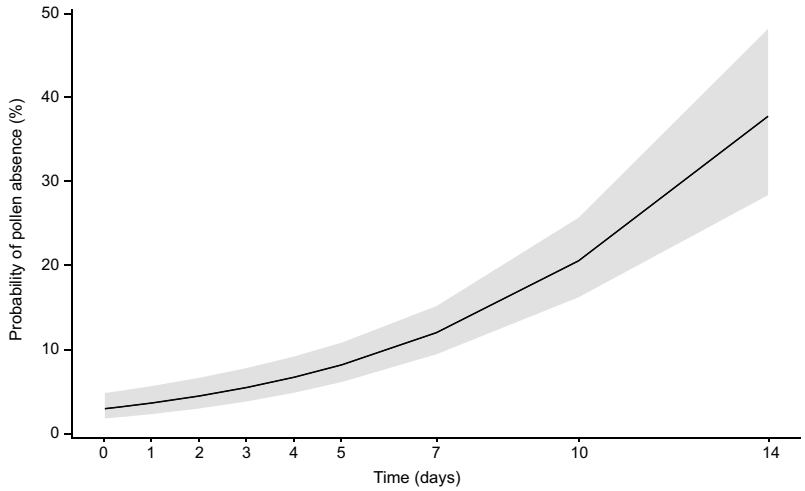

FIGURE 2 Relationship between the probability of finding a *Chrysoperla carnea* adult without pollen and time after feeding. The line represents the fitted effect of time based on a binomial generalized linear model, the shading indicates the 95% confidence interval.

gut pollen contents. Ideally, the number of detected pollen grains should be considered to estimate the potential date of consumption based on the digestion curves.

Pollen from different plant species vary considerably in their nutritional value (Roulston & Cane, 2000), though little is known about how this variation influences lacewings (Nordlund et al., 2007). Low-quality pollen with little protein, such as *Helianthus* pollen (Nicolson & Human, 2013), is associated with poor ovarian development in bees (Human et al., 2007). We found that consumption of *Acer* and *Quercus* pollen was higher than of *Fraxinus* and *Helianthus*, suggesting that pollen with high protein concentration is preferred by lacewings. This difference was larger at 25 than at 20 °C, which could be explained by the higher energy demands of insects at higher temperatures. In line with findings of Alcalá Herrera et al. (2022), female lacewings consumed more pollen grains than males, which is likely related to the higher protein demands of females for egg production and the longer foraging activity shown by female predators (He et al., 2021).

Sex did not influence digestion rates. Even if females and males have different nutritional requirements, *C. carnea* has no sexual dimorphism (Henry et al., 2002) and thus the digestion process is likely the same for males and females. Despite the temperature × plant species interaction effect on pollen consumption, we found no significant difference in digestion rate at 20 vs. 25 °C. Lacewings use enzymes to digest pollen (Li et al., 2010), which may be more effective at high temperatures. Of course, our two test temperatures may have been (equally) close to the optimum for enzyme activity, and lower temperatures, as experienced during spring nights or in winter, may have a stronger impact on digestion rates (Crailsheim et al., 1993).

A potential limitation of our study is that lacewings were relatively inactive during and after feeding due to the confined space in a Petri dish. In field situations lacewings are active fliers and they consume other food resources such as nectar or honeydew (Canard, 2001). Thus, field populations of lacewings could either have higher digestion rates than laboratory animals to meet their elevated energy demand, or lower digestion rates because of a possible physiological trade-off between high activity of the flight muscles vs. high activity of the digestive tract. Future studies using large cages or wind tunnels will allow testing of how movement affects digestion rates. Another aspect that might influence our results is that lacewings were offered pure pollen, which may lead to higher consumption than when feeding on flowers. However, Alcalá Herrera et al. (2022) offered flowers to lacewings in similar experimental conditions and the number of pollen grains was comparable to the number in our positive controls. Furthermore, inclusion of pollen from more plant species would be good to determine the relevance of the nutritional content or the structure of the grains on pollen digestion (e.g., smaller and larger grains than those studied here, different openings and wall widths). Finally, the number of lacewings available for each factor combination was relatively low. Nevertheless, we used a regression approach and the level of replication was sufficient for the data to support our conclusions.

In conclusion, we found that *C. carnea* lacewings consumed higher amounts of high-protein pollen grains and that females consumed more pollen than males. Pollen digestion rates differed among plant species and were faster for *Acer* than for other pollen types, leading to shorter pollen residence times for *Acer* pollen in lacewings' guts. Pollen digestion took long enough for pollen to be detected even 2 weeks after consumption in most individuals. The variable digestion rates of pollen grains may influence the study of lacewing diet composition. Studies that make inferences about the pollen diet or movement ecology of lacewings by analysing their gut contents should account for species-specific pollen digestion rates.

AUTHOR CONTRIBUTIONS

Ezequiel González: Conceptualization (equal); funding acquisition (equal); methodology (equal); formal analysis (lead); writing–review and editing (lead). **Felix J. J. A. Bianchi:** Conceptualization (equal); funding acquisition (equal); methodology (equal); writing – review and editing (equal). **Sarah Wizorek:** Formal analysis (supporting); investigation (equal); methodology (equal); writing – review and editing (supporting). **Mia Schumacher:** Formal analysis (supporting); investigation (equal); methodology (equal); writing – review and editing (supporting). **Martin**

H. Entling: Conceptualization (equal); funding acquisition (equal); investigation (equal); methodology (equal); project administration (lead); writing – review and editing (equal).

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DATA AVAILABILITY STATEMENT

Raw data is available upon request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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